ECOLOGY OF THE FAUNA OF FOREST SOILS

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A review is given of the meso- or meio-fauna, and to a lesser extent of the macrofauna of forest soils, with particular reference to population structure in mull and mor habitats; the influence of these environments on the fauna, and the role of the fauna as a factor in the establishment and maintenance of these conditions are also discussed. Numbers, biomass and 'activity' in mull and mor are contrasted. Population densities, without ancillary data, can give a very false impression. Biomass estimates provide important additional information, but the ultimate object of quantitative studies should be a measure of the 'activity' of the fauna. Mor tends to have large numbers of small species; mull is faunistically richer with smaller numbers and greater biomass. The pedological and biotic factors involved in mull and mor formation are briefly discussed. Tree species appear to have an important influence, but ground vegetation may be decisive under certain conditions. High water content in the 'H' layer and perhaps lack of oxygen are suggested as being important factors in confining the fauna to a narrow surface and subsurface zone of the raw humus in heathland. Present evidence suggests that certain members of the meiofauna are important for the mechanical comminution of plant detritus, but very little is known of their biochemical role. Stress is laid on the sequential pattern in organic-matter decomposition, and the succession of fauna and flora associated with it. A critical assessment of the importance of the fauna is at present hardly possible, but evidence would suggest a mutualism between vegetation and fauna, with the proviso that the vegetative change must come first. A plea is made for a closer co-operation between soil biological and pedological research.

INTRODUCTION

The term 'soil fauna' refers to all forms of animal life which at some stage in their life-history live on or within the soil. Zoologists have divided this fauna into three groups (FENTON, 1947): microfauna, mesofauna or meiofauna (MURPHY, 1953a) and macrofauna. These highly arbitrary groupings are based partly on size and partly on methods used for assessment and study. The microfauna includes such organisms as Protozoa, smaller Turbellaria, Rotifera, Nematoda and Tardigrada. The meiofauna, with a size range of about 100 microns to 1 cm, embraces the Enchytraeidae, most Arachnida, some Myriapoda and the smaller insects. The macrofauna includes Mollusca, Lumbricidae and the larger arthropods. The meiofauna, and to a lesser extent the macrofauna, are the main concern of this paper.

Both in respect of numbers of individuals and numbers of species, the Acarina or mites and the Collembola (springtails) are the most abundant soil arthropods. They are amongst the most widely distributed animal groups and occur in practically all situations where vegetation is growing. They may be found in a great diversity of habitats ranging from tropical rain forests (WILLIAMS, 1941) and deserts (TRÄGÅRDH, 1905), through the temperate zone to the Arctic tundra (HAMMER, 1944, 1952). They are present at high altitudes in the mountains (FRANZ, 1943, 1944), and are early colonizers of embryo soils (KÜHNELT, 1942, 1950) where they join with minute representatives of the plant kingdom in the long process which gradually builds up the soil surface.

In common with many soil creatures they tend to avoid light and to display marked thigmotactic responses. Many species show special adaptations to assist them in their life in this specialized substrate: there is frequently a dorso-ventral flattening of the body, reduced leg-size, and other characters which wed them to their habitat.

Naturally we associate the major part of the fauna with the organic material present in the soil, and under forest conditions the distribution of the latter is represented by two very distinct types which are usually referred to as ' mull ' and ' mor '. P. E. MÜLLER (1879, 1884), the Danish ecologist, first drew the forester's attention to these formations. He considered that the principal agents in mixing organic material with the mineral soil—the characteristic of mull—were earthworms. In mor, on the other hand, earthworms are absent as a rule, and consequently the organic matter forms a discrete layer on the soil surface.

Figure 24 illustrates the main characteristics of these two formations. The mor profile has a clearly defined organic deposition on the surface, and it is usual to divide this into three regions. The first or litter layer (Förna) consists of the unaltered dead remains of plants and animals. Beneath is the ' F ' layer (HESSELMAN, 1926; from the Swedish *förmultningskiktet*) consisting of leaves and other organic detritus which have undergone some comminution, but the source of the individual parts are still largely recognizable. The ' H ' layer (Hesselman, *loc. cit.*: *humusämneskiktet*), with a sharply defined lower boundary resting on the mineral soil, is composed of an amorphous material which has completely lost its original character and structure. Usually the mineral soil displays, in varying degrees, the characteristics of a ' podzol ', with an upper leached horizon (A_2) ashy-grey in colour and a lower zone of deposition (B), the appearance of which will depend on the nature

of the material eluviated from the ' A ' horizon. In contrast, mull has a thin scattering of litter on the surface, the ' H ' and frequently the ' F ' layers are absent, and the mineral soil has a high organic-matter content and good crumb structure. In this paper the term ' raw humus ' is used to describe the ' F ' and ' H ' layers of the mor; the word ' humus ' is reserved for the residues of organic decomposition present in mull soils.

Soil type, with some exceptions, does not directly affect the formation of mull or mor but rather exercises an indirect influence, inextricably merged with vegetation type (litter-source) and

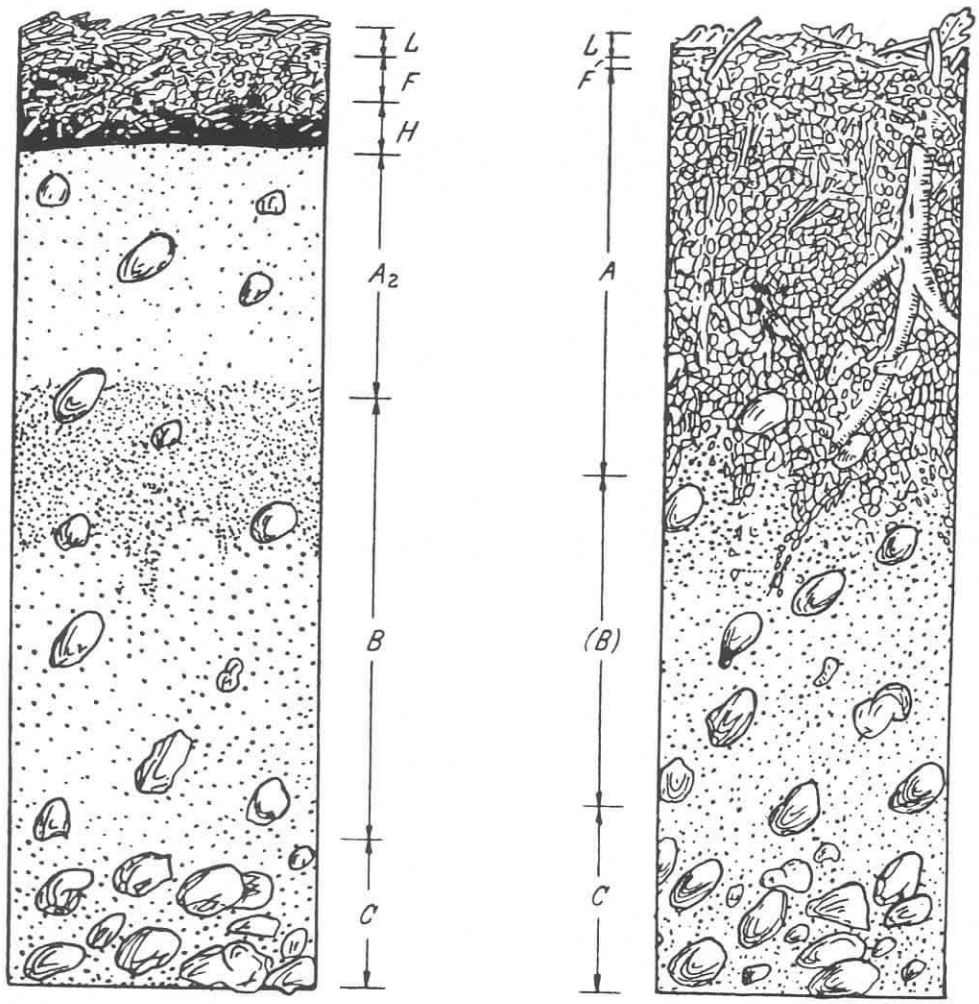

Figure 24—Schematic diagram of mor (left) and mull (right) profile (modified after Fenton, 1947).

A, mineral horizon with incorporated organic material, that is mull formation; A_2, leached mineral horizon; B, illuvial horizon; (B), mineral horizon with paler colour and lower organic matter content than A; C, parent material; F, fermentation layer; H, layer of humus formation; L, litter layer.

physiography of the site. It should be stressed that the two terms, as used here, represent the extreme conditions; there is an infinite series of gradations occurring between.

The central theme of this paper is an endeavour to contrast the fauna and environments in these two habitats. Some examples are drawn from a heathland area, a good example of extreme mor conditions. This is partly because some of the writer's own studies are concerned with this habitat, and also because there are some very interesting pedological data available (RENNIE, 1951, and unpublished) which can be related to the faunal structure.

QUANTITATIVE ASPECTS OF SOIL FAUNAL POPULATIONS

In any examination of the fauna of a soil habitat the most obvious feature is the vertical distribution in the profile: an example from a heathland study (Murphy, 1953a) will serve as an illustration of this situation under mor conditions. *Figure 25* contrasts the arthropod population of natural heathland (Allerston Forest area, north-east Yorkshire) with that of cultivated heathland (same area) planted with *Picea sitchensis* (trees 20 years old and forming canopy). The populations are those quoted in Table 4. The heathland profile is a podzol with a shallow litter and raw-humus horizon (total about 2 inches), and a very distinct, thin iron pan some $6\frac{1}{2}$–7 inches below the surface. The dominant vegetation is *Calluna vulgaris*. The totals in the various horizons should be treated with caution owing to the great variation from sample to sample. They should be regarded merely as a broad indication of the vertical population structure.

The most conspicuous property of this distribution is the great compression of the arthropod population in the natural heathland, 96 per cent (9·6 animals per cm^3) being concentrated in the first $2\frac{1}{4}$ inches. The remaining 4 per cent (0·1 per cm^3) is scattered through the profile and shows no local concentration except in the organic matter just above the pan. The maximum density, 28·1 arthropods per cm^3, occurs in the first quarter to half inch of the raw-humus horizon. In mull, on the other hand, the general tendency is to have a more even vertical distribution, but unfortunately there is no recent comprehensive analysis to illustrate the point. However the figures of SALT and his colleagues (1948) give an indication of what might be expected in a grassland with a mull profile (Table 4). They found that 67 per cent of the Acarina and Collembola occurred in the 0–6 inch, and 33 per cent in the 6–12 inch zones.

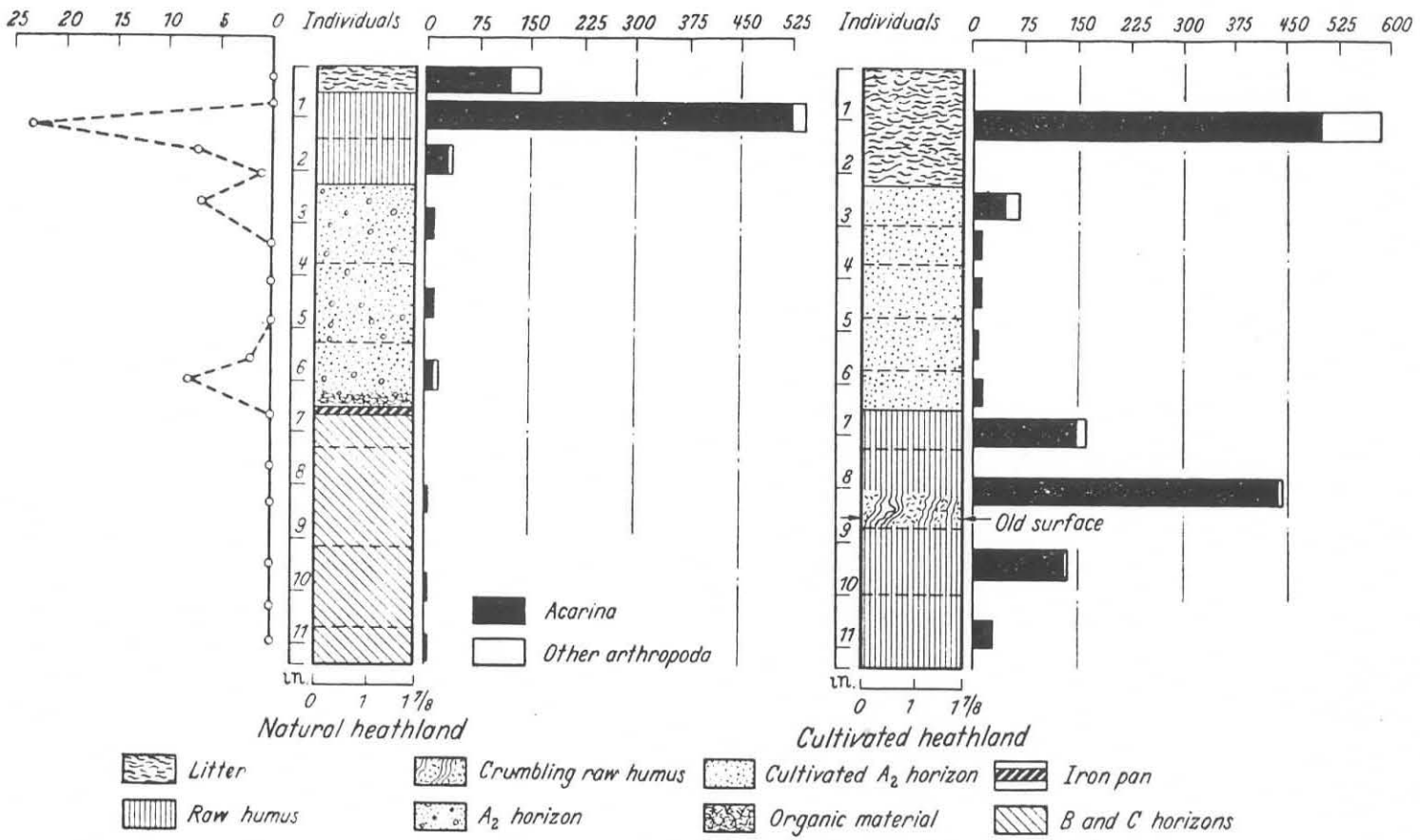

Figure 25—The vertical distribution of soil arthropods in natural and cultivated heathland (planted with Picea sitchensis *Trautv. and Meyer). The graph on the left illustrates the distribution of a mite belonging to the Acaridiae in the natural heathland (see page 115). Sample in each case is a cylinder $1\frac{7}{8} \times 11\frac{3}{8}$ inches deep with a volume of 506 c.c. (Corrected after Murphy, 1953a).*

4,7 cm × 28,4 cm

When considering the quantitative distribution of the fauna it must be remembered that many soil organisms are not distributed at random but show an aggregated pattern; *Figure 26* is an illustration from the above mentioned heathland. Six samples were obtained from a raw-humus sod 25 × 15 cm in size, each sample having a surface area of 17·8 cm² and a depth of 4 cm, and together representing about 30 per cent of the total area. The numbers range from 87–406 Acarina per sample. Part of the increased population occurring at one end of the block is due to a massed occurrence of very small mites belonging to the genus *Tarsonemus* (120–140 microns long). Indeed this example with a comparatively simple faunistic structure may be less extreme than that occurring in more diversified habitats.

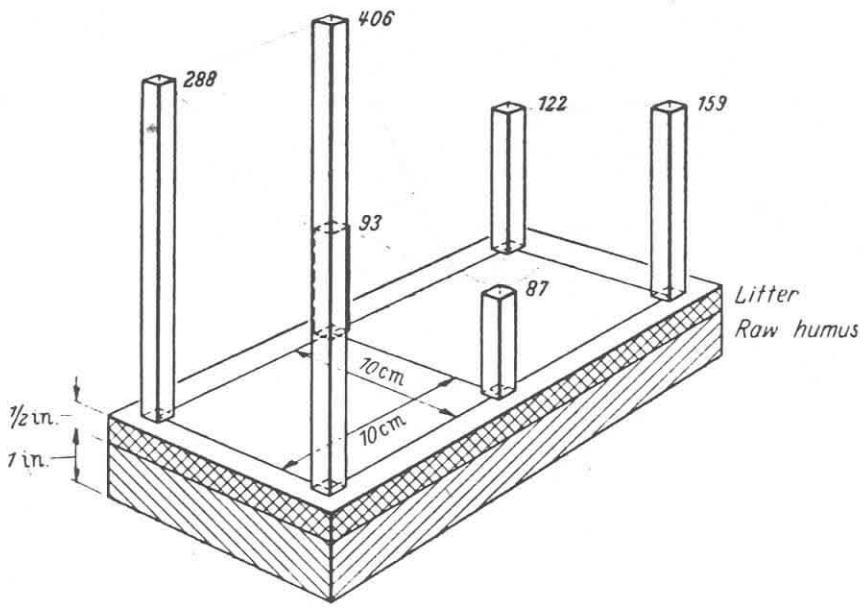

Figure 26—Numbers of Acarina present in six natural heathland samples of litter and raw humus spaced 10 cm apart. Sample diameter 1⅞ × 1½ inches deep with a volume of 68 c.c.

Bearing in mind this fact, and making the additional qualification that there is a considerable seasonal fluctuation in numbers, it is worth while considering the size of population to be expected in various situations. Table 4 compares the most recent British figures for arthropod numbers from natural heathland, cultivated heathland with trees, a young conifer plantation (*Picea sitchensis*), fenland, grassland and arable land. The data of Macfadyen, Evans and Baweja are means of 12 monthly samplings, whilst the grassland figures represent the mean of 9 samples obtained in

November. A most striking feature is the large numbers present in heathland and the meagre numbers in cultivated sites; the former are believed to be the highest yet recorded in Great Britain. It should be stressed, however, that they represent populations occurring in November at a time when they tend to build up to a peak. The small populations of arable land may be a reflection of technique, although there is a general impression that soil disturbance causes major reductions. It would be unwise to attach too much importance to these data since there is not yet sufficient information to provide a comprehensive picture of population densities, but they are the best at present available.

TABLE 4

Total populations of soil arthropods in heathland and other habitats in Great Britain

Author	*Habitat*	*Total sample depth (in)*	*Numbers per sample*	*Numbers per m² (thousands)*	*Numbers per cm³*	*Sample volume (cm³)*
Murphy (1953a)	Natural heathland (maximum)	11⅜	998	569·7	1·97	506
	Cultivated heathland with trees (maximum)	11⅜	1,462	834·5	2·89	506
Evans (1950)	Spruce plantation	2½	313	154·6	2·42	130
Macfadyen (1952)*	Fenland	2	159	159·4	3·18	50
Salt *et al.* (1948)	Grassland	12	2,756	340·5	1·15	2,471
Baweja (1939)	Arable land	9	201	25·9	0·11	1,770

* Acarina and Collembola only.

Apart from EVANS (1951) and Murphy (1953) there have been no published studies of forest soils in Great Britain. Table 5 outlines the populations in other European countries of meiofauna and macrofauna in beech on mull and in beech and spruce on mor. The small number of surveys tabulated is due to the difficulty of comparing data because of different methods of expressing population numbers, and even in these examples there is a degree of approximation owing to this. There is no doubt that a standard method of presentation to allow of comparisons is highly desirable, and indeed essential, if the greatest possible amount of information is to be obtained from this arduous form of research.

It is not possible here to do more than draw attention to the salient features of these studies (but see Murphy, 1953a). The investigations have the common feature of increasing population estimates with improving methods. BORNEBUSCH's (1930) maximum of 19,400 arthropods per m^2 is rendered insignificant by FORSSLUND's (1945) formidable total of over a million per m^2. Yet despite this large total, under certain conditions it may be a gross underestimate of the actual density, for Forsslund (1947) has examined directly small samples and has obtained a population equivalent to 2,300,000 arthropods per m^2. Whilst it would be unwise to regard this as a true estimate owing to the methods used in sample selection *etc*, it represents a twofold increase on the maximum figures already quoted.

TABLE 5

Total populations of meiofauna and macrofauna in European forest habitats

Author	*Habitat*	*Total sample depth (in)*	*Numbers per sample*	*Numbers per m^2 (thousands)*	*Numbers per cm^3*	*Sample volume (cm^3)*
Bornebusch (1930) (Denmark)	Beech mull	4 (?)	619	6·2	0·06 (?)	10,000 (?)
	Beech mor	6½ (?)	1,943	19·4	0·11 (?)	17,000 (?)
	Spruce mor	5	1,194	11·9	0·09	13,000
Ulrich (1933) (Germany)	Beech-oak mull	—	1,938	—	1·94	1,000
	Spruce mor	—	2,260	—	2·26	1,000
Forsslund (1945) (Sweden)	Spruce-pine-birch mor	4	1,184 1,430	1,089·6	10·90	400 100
Drift (1951) van der (Netherlands)	Beech mor	1½	1,033 214	336·5	8·79	40 4,000

Various authors have drawn attention to the drawbacks inherent in Bornebusch's pioneer study; nevertheless it provides a general indication of the quantitative differences existing between mull and mor. Comparison of his two beech sites shows the inverse relationship between size and number of animals in these two habitats; the mor contained a large number of small organisms and was, in addition, a faunistically poorer biome.

It is clear that a purely quantitative comparison can give a very misleading picture. What is required is an estimate of the biomass of fauna, a measure necessary to integrate size and number and thus

to provide a clearer conception of the living material available. For present purposes, biomass can be defined as the weight or volume of the population per unit area or unit volume depending on the data available. Several investigators have attempted this measurement, but owing to the shortcomings of present experimental methods their results probably diverge from the absolute values to a considerable extent. Table 6 represents the biomass figures of some of the surveys already quoted in Tables 4 and 5. The estimates in all cases were obtained directly by weight or measurement. Bornebusch's totals, although too low on an absolute scale, provide an interesting illustration of the relative differences between mull

TABLE 6

Biomass of soil meiofauna and macrofauna in various habitats
(For other details see Tables 4 and 5)

Author	*Habitat*	*Total fauna Biomass per m²*		*Acarina and Collembola*			
				Numbers per cm³	*Biomass per cm³*		*Ratio of living matter to litter volume*
		Volume cm³	*Weight g*		*Volume mm³*	*Weight mg*	
Bornebusch (1930) (Denmark)	Beech mull	—	70·77	0·04 (?)	—	0·0029 (?)	—
	Beech mor	—	16·57	0·10 (?)	—	0·0056 (?)	—
	Spruce mor	—	9·84	0·08	—	0·0045	—
Ulrich (1933) (Germany)	Beech-oak mull	—	—	1·84	0·032	—	1:31,000
	Spruce mor	—	—	2·12	0·034	—	1:29,000
Forsslund (1948)* (Sweden)	Spruce mor	—	—	14·6	0·052	—	—
Drift (1951) van der (Netherlands)	Beech mor	11·20	—	8·61	0·087	—	1:33,000
Macfadyen (1952) (England)	Fenland	—	—	3·19	0.027	~~0·027~~	1:37,000

* Not the same site as quoted in Table 5.

and mor. Beech mull has a total of 70·8 g per m² of which 53 g consist of earthworms. In beech mor the total is 16·6 g, and this reduction is primarily due to the small number of earthworms, which weigh only about 1 g per m². It will be noted that the Acarina and Collembola figure for mor is almost double that for mull, although inadequacy of method may have a great effect on this component of the population.

The last column of Table 6 gives some indication of the spatial relationships of the litter fauna in terms of volume of litter material.

These figures suggest the interesting conclusion (with reservations) that the total biomass of Acarina and Collembola shows no great difference in the upper litter layers of beech mor and spruce. Van der Drift's (1951) total for these groups in the litter and raw humus is equivalent to 1:11,000, and his maximum which occurs in the 'F' layer, 1: 5,000. The ratio from Macfadyen's data, 1: 37,000 (assuming a specific gravity of 1), indicates that the fenland biome compares rather unfavourably with the raw-humus layers of a beech forest.

Reference has already been made to the population structure of a mull grassland (Salt and his colleagues, 1948), and an estimate of the biomass would be of interest to compare with the rather extreme mor sites already discussed. Considering only the smaller arthropods (mainly Acarina and Collembola), they estimate an average volume per individual of 0·05 mm^3 (Van der Drift's corresponding figure is 0·01 mm^3), which is equivalent to 1 part living matter to 20,000 parts soil. When compared with the figures already quoted this seems a very reasonable estimate, and bearing in mind the sample depth of 12 inches probably points to a very much greater proportion of living material than would be present in a beech mor. To sum up, therefore, present data would suggest the following proportions—expressed as volumes—for the acarine and collembolan fauna:

litter layer in the forest	about 1: 30,000
raw humus	about 1: 10,000–20,000
grassland to 12 inches deep	about 1: 20,000

The quantitative estimation of the importance of the soil population is the obvious goal of the investigator. Population numbers without ancillary data can give a very false impression of the fauna of a particular habitat. Biomass values appear to rest on a surer foundation, but they give no indication of the 'activity' of the fauna, and indeed they can be misleading, for Bornebusch has shown in his respiration experiments that oxygen intake, and therefore food consumption, per unit of body weight, is less for large than for small soil animals. Table 7 summarizes his data figures for numbers, biomass and oxygen consumption for the localities already discussed (Tables 5 and 6). It is likely that these have a significant relative value, but the absolute values are unsatisfactory. In the beech mull earthworms constitute 75 per cent of the biomass and 55 per cent of the total oxygen respired; in beech mor the figures are respectively 7 and 3·5 per cent. On the other hand, Acarina and Collembola in beech mor represent 5·7 per cent of

TABLE 7

Numbers, biomass and oxygen consumption of meiofauna and macrofauna in Danish forest soils (Bornebusch, 1930)

Habitat	*Numbers per m²* (*thousands*)	*Biomass per m²* (*g*)	*Oxygen consumption per hour at 13°C* (*mg*)
Beech mull	6·2	70·77	19·73
Beech mor	19·4	16·57	11·97
Spruce mor	11·9	9·84	7·09

the biomass and 27·1 per cent of the respiration total, the equivalent figures for spruce mor being 6·0 and 25·4 per cent. These relationships are illustrated graphically in *Figure 27*, where the data are expressed as percentages of the total for mull and mor. Within each habitat there is a negative correlation between number and mass of fauna, the direction of this relationship being reversed when mull and mor are compared. In other words, the products of these values in each case tend towards constancy. The biomass

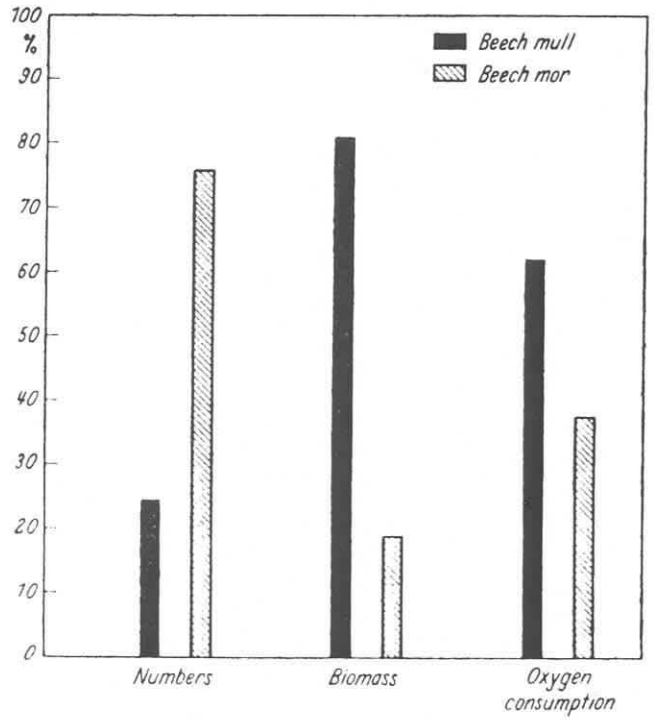

Figure 27—Numbers, biomass and oxygen consumption of meiofauna and macrofauna in beech mull and mor (data from Bornebusch, 1930). In each case figures are expressed as a percentage of total for mull and mor.

and oxygen consumption for mor are respectively 19 and 38 per cent of the total for mull and mor. Indeed the respiration per gramme biomass is over $2\frac{1}{2}$ times that of the mull, which quite obviously underlines the statement already made concerning size of organism and its ' activity '.

To some extent a consideration of a measure of the ' activity ' of the soil fauna is at present theoretical. Nevertheless it should be possible to make reliable estimates when suitable techniques are evolved (MACFADYEN, 1948) and the necessary data have been accumulated to provide overall values for groups of the soil population. It is important to bear these considerations in mind when carrying out quantitative studies for there is not much point in tediously accumulating such records if they cannot be utilized when the goal of ' activity ' measurement is more fully realized.

Finally let us contrast the attributes of mull and mor from the point of view of population numbers. On the one hand we have in mull larger organisms, greater biomass and diversity, a greater depth of substrate inhabited, and therefore a more equable distribution of the primary environmental factors, living space, oxygen, water and food, the results of which are a constant interchange of materials from surface to interior and *vice versa*. Mor, on the other hand, is an impoverished system with smaller organism and smaller biomass; members of its fauna have little mechanical influence on their medium. They live in an environment of organic remains, a separate, discrete layer, and are cut off from the mineral soil beneath. This population compression creates a vicious spiral which embraces in a stranglehold grip the living material of the mor, and leads to a contracting milieu, an ever-narrowing zone of life.

PEDOLOGICAL PROPERTIES OF MULL AND MOR

The number of firmly established facts about these two formations are few. Mor is characteristic of well-drained, acid habitats (pH 3–6·5), especially heathland and coniferous forests. In these soils the amount of available calcium is low, nitrates can hardly be detected and ammonium nitrogen is present in very small quantities. Mull typically occurs with mixed or deciduous forests on moderately well-drained soils. The acidity range is normally pH 4·5–8, there are reasonable supplies of calcium, and the amounts of ammonium and nitrate nitrogen are greater than in mor soils.

Müller regarded mull and mor as biological and not purely physico-chemical systems, and considered that the fauna present was an important tool in the formatory process. A few have followed up Müller's findings in the light of present knowledge.

but many pedologists have stressed physical and chemical rather than biological mechanisms. Mor has been regarded as a situation where organic matter is accumulating, and there has been much discussion of *rate* versus *type* of decomposition in typical profiles. However, as ROMELL (1932) has ably demonstrated, the differences in amount of organic matter may not be so very great if they are expressed on a volume rather than weight basis.

The theory that type rather than rate of decomposition is the important criterion is an attractive proposition when soil organisms are considered. In mor nitrifying bacteria may be absent, and it is thus suggested that under the usually acid conditions of mor the main decomposing agents are fungi, not only free-living species but also mycorrhizal forms associated with plant roots. In mull there is less acidity, a more equable base status, and bacteria tend to replace fungi. There is a greater volume of soil inhabited by flora and fauna, and nitrogen is not a limiting factor. There is also the suggestion (Kühnelt, 1950) that under these conditions soil organisms prevent the development of fungi of a strongly competing type, and this is a plausible hypothesis in situations which might oscillate between mull and mor with small changes in one or two vital factors.

There is evidence that acidity in mor is not merely due to leaching of bases and extreme unsaturation of the humus colloids, but to actual production of acids, for example by fungi (Romell, 1935), and that if organic acids are formed, their effect upon acidity must depend very much on nitrogen status. It may be argued further that if type of decomposition is the real criterion—and there is evidence that it is so—then, practically speaking, different types of ' humus ' are being elaborated in each case by different biological complexes, and that an understanding of nitrogen status and mode of utilization may prove the keystone to the problem. HANDLEY (1954) has found that under mor conditions the vascular cells of the leaf disappear first, leaving behind a residue of mesophyll tissue; in mull-forming litter the reverse is the case. From experimental evidence he suggests that leaf-litter proteins have been stabilized by protein-precipitating materials, and in some cases they are extremely resistant to decomposition. This process would appear to be an important factor in the accumulation of partly undecomposed mesophyll elements.

The influence of biotic factors, especially vegetation, appears particularly important when the reversibility of the mull-mor system is considered. There are many well authenticated instances of changes in either direction when the only obvious alteration is the

plant species growing on the site. Certain species are associated with both mull and mor—beech is an outstanding example—and this would suggest that the litter source might not be so important in the development of these humus forms. However, it is often overlooked—although frequently stressed by TAMM (1920) and others—that the ground vegetation (including mosses) associated with a tree species may provide a considerable part of the plant detritus. Mull associated with a herb flora under spruce (Tamm, 1920) is a case in point, and TANSLEY (1949) refers to the abundance of certain bryophytes and lichens where mor develops under beech. Tansley further suggests that much of the organic material in heathland may be derived from similar plants growing beneath the *Calluna* canopy. With mor development under beech it is likely that, at least in certain cases, the tree litter plays a relatively minor role in initiating mor formation, since a prerequisite for good moss cover is a surface devoid of litter; BROWN (1953) points out that the best examples are usually found in situations where wind has scattered the beech leaves.

TABLE 8

Pore volumes of natural and cultivated heathland (after Rennie, 1951)

Habitat	*Horizon depth (in)*	*% total porosity*	*Winter 1949–50*		*Summer 1950*	
			% air	*% water*	*% air*	*% water*
Natural heathland						
Raw humus	0–1½	75	9	66	39	36
Brownish-grey bleached horizon	2–7½	52	8	44	26	26
Cultivated heathland						
Inverted bleached layer	3–8	45	10	35	23	22
Inverted raw humus	8–10	75	32	43	42	33
Undisturbed raw humus	10–12	70	25	45	40	30

SOIL ENVIRONMENT AND ITS INFLUENCE ON FAUNA

Living-space, water, oxygen and food are the most vital requirements of the soil fauna, and a brief consideration of these factors may suggest some reasons for the differences in population structure already demonstrated. Amount and kind of soil pore-space is of prime importance because it not only determines the nature of the living space but also has a very great effect on the humidity and gaseous conditions of the environment. Kühnelt (1950) suggests that there is a relationship between the average size of the soil

interstices and the meiofauna inhabiting them. Thus he states (quoting an unpublished study of Wittasek) that, in loose soils with crumb structure, large species of Oribatei are found, in contrast with the smaller forms of compact soils such as heavy clay meadow habitats.

Unfortunately pore-volume and size-distribution data of sites which have been investigated for soil fauna are very meagre. Table 8 outlines determinations for the heathland area already discussed. The raw-humus horizon is extremely rich in living-space, but many of the cavities are very small. This may affect the qualitative structure, for it is noticeable that the commoner Oribatid genera are represented by their smallest species (Murphy, 1953). It might also be an explanation for the large numbers of Prostigmata, and relative scarcity of Collembola, which rarely constitute more than 20 per cent of the population. The largest numbers of the latter (Table 9) were recorded from a sample with clearly differentiated ' F ' and ' H ' layers, and, as the presence of an ' F ' layer is unusual in this heathland, it is possible that their small numbers may be due to the fact that their size range does not descend to the level of the smallest species of Acarina.

TABLE 9

Total Acarina and Collembola in raw-humus sample with clearly defined ' F ' and ' H ' layers

	Depth (in)	*Acarina*	*Collembola*	*Numbers per m² (thousands)*
Litter	1–0	214	12	91·9
Raw humus	0–2	347	342	280·2
Total		561	354	372·1

It would be misleading to overstress living-space *per se* as a possible limiting factor under mor conditions. More important is a consideration of the humidity and gaseous conditions of the environment, attributes which are linked with and sometimes controlled by pore-space content. The heathland raw humus has a high moisture content even during dry periods (Table 8). In the leached zone, on the other hand, the water content can be low even during the wet season, and this condition persists more or less to the deeper

layers. It seems therefore that the surface organic material when completely saturated prevents the passage of water to the mineral soil, and thus acts as a discrete, blanket-like layer. During wet weather surplus water flows over the surface and collects in low-lying depressions. From the point of view of the fauna, water may be an active competitor for living-space, and this is supported by the vertical distribution (*Figure 25*), the zone affected to the greatest degree being the lower part of the ' H ' layer.

The faunal distribution in the cultivated profile (*Figure 25*) is further evidence of this competitive effect. The cultivation is of a rather special type and is not equivalent to a simple surface disturbance. A furrow is ploughed out, one for each row of trees, the furrow being turned on to the undisturbed surface and the trees planted on the side of the ridge so formed. The result is that the two raw-humus horizons are brought together to form a ' sandwich '; the distribution illustrated in *Figure 25* is a vertical section across the centre of one of these ridges. The population of the sandwich, 53 per cent of the whole (3·6 per cm^3), is quantitatively and qualitatively different from the undisturbed heathland. There is a more even distribution of fauna through the raw humus, and the air and water percentages (Table 8) suggest that more equable environmental conditions prevail in the cultivated profile.

From the point of view of the fauna, the humidity of the cavities is of great importance. THAMDRUP (1939) has ascertained the relative humidity of the raw humus of a Danish heathland and has found that a moisture content of 10–20 per cent (dry matter + water = 100 per cent) corresponds to a relative humidity of 75–90 per cent. He considers that even under very severe drought conditions (moisture content of about 30 per cent), the relative humidity does not fall below about 90 per cent. This evidence corroborates the view that low humidity is rarely a limiting factor in the ' F ' and ' H ' layers of this particular habitat.

The figures for percentage pore-space filled with air and water are divided into winter and summer values, but the latter operate for a very short period, and usually at a time when population numbers are at their lowest level. The winter data indicate that only 9 per cent of the volume of raw humus of the natural heathland is available to aerobic organisms, the population being 7·4 per cm^3 of the gross volume (excluding litter), 9·9 per cm^3 of the total pore-space, and 82·2 per cm^3 of gas-filled pore. It is also worth noting that though the total pore volume of the mineral soil is only two-thirds of the raw humus value, the gas-filled pore almost equals the raw humus.

Unfortunately there is no information concerning the gaseous composition of the raw-humus environment, but a possible pointer to the oxygen status of heathland may be obtained by a consideration of the vertical distribution of a new species of *Schwiebia*. There is little known of the biology of this genus, but other members of the Acaridiae, to which it belongs, for example *Tyroglyphus farinae* L., can live under conditions of low oxygen and/or high carbon dioxide concentration (HUGHES, 1943). Examination of the vertical distribution of the *Schwiebia* sp. (*Figure 25*) shows a peak just below the main faunal concentration in the raw humus, which decreases to zero at the base of this horizon. A small number occur in the upper portion of the 'A_2' horizon, and there is a further concentration in the organic matter just above the pan. In this particular profile it was the only mite occurring in numbers below $1\frac{1}{2}$ inches; the other organisms present were subterranean Collembola; Kühnelt (1950) suggests that these species can also live in conditions of low oxygen. Whilst the writer would not wish to draw too much from this distribution pattern, there is a suggestion that excess water and lack of aeration may be limiting factors, and that this rather sluggish species, perhaps because of competition or predatory enemies, is perforce driven to a part of the profile inhabited by few other mites.

ROLE OF THE FAUNA IN THE LIFE OF THE SOIL

With some exceptions, knowledge of the habits of the soil fauna and the physical and biochemical influence on its medium is very meagre. Very little research has developed beyond the population-study stage, but such facts as the large populations present in the litter and 'F' layers and their apparently saprophagous and fungal feeding-habits point to the need of investigation of their role as a link in the biochemical chain whereby organic material is broken down and its constituents released for re-utilization.

The direct, mechanical effect of the meiofauna on its environment is probably small. The animals are, to a degree, bounded by the larger soil and litter interstices and their movement almost entirely depends on the presence of channels and pores formed by other agencies. Indirectly, however, they may increase aeration and drainage insofar as they eat out decayed roots and thus leave manured channels in the soil (GILYAROV, 1947; ROGERS, 1939), an effect perhaps of greater importance under grassland conditions.

Of the mites and springtails, it is probable that the majority are saprophagous and fungal feeders. Forsslund (1939) and SCHUSTER (1955) have examined the gut contents of some Oribatid mites and

found fungal mycelia present. Others are known to feed on decaying leaves of plants, and JACOT (1939) recorded the presence of nymphs of certain Phthiracaridae burrowing within conifer needles where they apparently spend a considerable portion of their early life. The writer (Murphy, 1952) has observed this phenomenon in laboratory cultures. RIHA (1951) has shown that some species feed on decaying wood.

TABLE 10

Areas of ash and birch consumed by *Steganacarus magnus* (Nic.) (see Murphy, 1952)

Leaf disc presented	*Area* mm^2	*Area consumed complete perforations* mm^2	*Consumed* %	*Area partially consumed* mm^2
Ash disc A	23·8	11·0	46·3	—
Ash disc B	23·8	12·5	52·8	—
Birch disc A	21·7	3·6	16·6	1·2
Birch disc B	21·7	3·9	17·9	0·4

The influence of vegetation in mull and mor formation, and the fact that litter-feeding species are of importance in determining to some degree the end-point of the decomposition cycle renders experiments to ascertain the palatability of litter of different tree species a valuable study. Various investigators have carried out experiments of this nature in the laboratory with earthworms (LINDQUIST, 1941; FRANZ and LEITENBERGER, 1948; Franz, 1950), millepedes (LYFORD, 1943; Franz and Leitenberger, 1948), mites (NOORDAM and DE VLIEGER, 1943; SPENCER, 1951; Riha, 1951; Murphy, 1952; Schuster, 1955) and Collembola (SCHALLER, 1950). Spencer found that litter-feeding mite species showed a marked preference for broadleaf as opposed to conifer litter, and ash to birch. These preferences have been confirmed by further experiments carried out by the writer (Murphy, 1952). After 96 days a population of approximately 75 *Steganacarus magnus* (Nic.) mites consumed about 50 per cent of the ash and 17 per cent of the available birch litter (Table 10). Most culture experiments with the Oribatei have been concerned with adults, but it is probable that the immature forms of this group are of greater importance. Riha (1951) has pointed out that adults of some species leave the litter and soil layers to reach suitable oviposition sites such as decaying tree stumps *etc* and it is possible that they spend a considerable portion of their lives in the task of dispersal. Larvae and nymphs, on the other hand, have been found to be extremely voracious feeders under suitable culture conditions.

The biochemical role of the soil fauna is at present extremely obscure. It is generally believed that the majority of the meiofauna cannot digest celluloses, hemicelluloses or lignins. Fungi, on the other hand, can oxidize these substances, and soil organisms, in turn, may feed on the protoplasm of some species of fungus. Their excrement, in its turn, provides a milieu for further decomposition by fungi, coprogenous organisms *etc.* BIRCH and CLARK (1953) stress the sequential pattern of organic-matter decomposition and the succession of organisms associated with it. They quote an interesting example (CLARK, 1949) where the succession of microfauna on decomposing *Casuarina* litter is determined to some extent by the presence or absence of faeces of larger organisms such as amphipods, which may have been feeding on the leaves. Some soil creatures will not feed on fresh litter, which lends weight to the argument that fungi or other agents perform a preliminary ' softening-up ' process before the fauna takes over. Much of this is mere conjecture, however, and further study may indicate the presence of a more comprehensive digestive equipment. TRACEY (1951), for example, has discovered the presence of the enzymes cellulase and chitinase in earthworms.* In addition, some members of the meiofauna may be able to degrade these substances by means of the microbial population of their guts.

The excrement of soil invertebrates provides an important substrate for further decomposition, and much of the soil organic matter may be present in this form under certain conditions (KUBIENA, 1943; see also page 73). Spencer (1951) examined microscopically the faecal pellets of the mite, *Steganacarus magnus* (Nic.). These averaged about 145×125 microns and, when crushed, were found to contain numerous leaf particles of 5×3 microns; very few fungal hyphae were seen. This indicates that, apart from any chemical transformations, the role played by these mites in the comminution of decaying leaf-tissue is of a high order.

CONCLUSION

Having endeavoured to contrast the attributes of mull and mor, an attempt will now be made to elaborate a general statement concerning the soil fauna and its contribution to these systems.

Vegetation appears to be the most consistent agent in deciding the type of organic-matter decomposition, and the associated faunal entities are of considerable interest. Certain plant species show well-marked tendencies to form mull or mor, and the leaf

* His suggestion that these were probably produced by the worms themselves requires confirmation —ED.

comminuters amongst the fauna show a preference for mull-forming plants. Where tree species, for example beech, are associated with both conditions it is possible that the ground vegetation is the more important organic-matter source. Even with such a pronounced mor former as *Calluna vulgaris* it is likely that lichens and certain mosses contribute a considerable amount of the detritus for raw humus formation. The writer (Murphy, 1953) has found that when *Nothrus silvestris* Nic. in laboratory cultures is provided with *Calluna* and Sitka spruce litter there is very little difference in preference, and quite large quantities of the former are consumed. It is well known that the mixing of a species, of which the litter is not readily humified, with more palatable types results in an amelioration of the overall humus conditions, though the processes involved are little understood (WITTICH, 1933). Field observations made by Spencer (1951) in conjunction with his laboratory experiments revealed very few *Steganacarus* mites under ash and birch, which suggests the hypothesis that some of these organisms may play a part in the more rapid litter decomposition which frequently occurs in mixed broadleaf and conifer stands. The accumulation of conifer needles may provide suitable environmental conditions, whilst the broadleaf litter provides palatable food material for the maintenance of litter-feeding populations of soil Acarina at a high level (Murphy, 1952).

There are many examples of the reversibility of the mull-mor process, in some cases the first obvious alteration being a change in vegetation, followed by the development of a different fauna. DIMBLEBY (1952) describes mull conditions developing under natural birch (*Betula pubescens*) in the Yorkshire heathland, and the writer (Murphy, 1951) has found the earthworm, *Lumbricus rubellus* Hoff. in young birch plantations in the same area. Even more outstanding examples can be found in marginal lands in north-west England (CROMPTON, 1953). Here earthworms are considered to be the main biological agents in the regeneration process. In each instance a change in vegetation or a chemical treatment followed by a change in fauna has resulted in a marked alteration in the profile, and it is probable that the new fauna becomes established within a very short period. In this connexion there is an interesting experiment in Yorkshire (Dimbleby, 1952), laid out in 1948, where suppression of *Calluna* and yearly applications of birch litter to the heathland resulted in very rapid faunistic changes. When sampled for meiofauna one year later (Murphy, 1951, 1952), there were considerable differences (mainly Mesostigmata, Collembola and perhaps Enchytraeidae) between treated

and control plots. Young birches are now growing on this site and earthworms have made their appearance (Dimbleby, personal communication, 1955). The swing over to a richer fauna may be achieved either by a very efficient dispersal mechanism—the writer has not found earthworms in the undisturbed heathland—or by an inherent reproductive potential which quickly takes advantage of the changed conditions, or indeed a combination of both. Whatever the mechanism, new species appear and existing ones increase in number.

The increasing faunal, and indeed floral, diversity when mor changes towards mull seems to be a point worth emphasizing. The diversity of fauna in a good mull soil may be one of its greatest assets because the humification process flows through a wide variety of organisms with varying metabolisms, and offers better opportunities for degradation of intractable materials. OVERGAARD NIELSEN (1949), whilst recognizing their part in humification, makes the interesting suggestion that the soil fauna's most important function is to act as a reservoir or buffer of easily available and rapidly circulating substances. From this point of view the qualitatively rich fauna of mull would further enrich its habitat. A further important point is that activity and movement of larger organisms in the profile will provide the microfauna and flora with a means of transport so that their chances of contacting suitable substrates are greatly increased.

Associated with these changes is an increase in diversity of habitat, and this would seem to be a necessary prerequisite for the maintenance of a faunistically rich soil population. Amongst the Acarina, for example, the presence of decaying wood is probably necessary for the development of large populations of certain Phthiracaridae, as the immature stages spend much of their early life in this material. Indeed the scarcity of these mites in the heathland may be due to the absence of such a medium. In recently cultivated profiles, sampled two years after ploughing, the writer (Murphy, 1954) has found numbers of a Ptyctima-mite, *Pseudotritia ardua* (Koch) and quite large amounts of excrement in the region where the two raw-humus layers meet. It is indeed remarkable that this species should be numerous in this ploughed profile and yet be completely absent from the undisturbed sample sites a few hundred years away. This mite feeds on litter, wood and decaying stems, and the active feeding taking place appeared to be due to the presence of dead *Calluna* stems buried during the ploughing process.

As implied in an earlier section of this paper, there is a widespread opinion that the fauna has little direct influence in these soil processes. Handley (1954), for example, in his searching analysis of the factors responsible for mull and mor formation, suggests at the outset that the processes involved in soil formation can only be understood in terms of a multivariable system; he is of the opinion that the fauna cannot be regarded as a determining factor. However, in cases of mor turning to mull there is good evidence to suggest that there is a step by step process, a change in vegetation followed by a change in fauna, but the fact that the latter appears to be an automatic development does not necessarily imply that it is incidental to the process. Rather there would seem to be an amalgam of these two factors, a mutualism with the proviso that the vegetative change must come first. This sequence of events is perhaps due to the greater freedom of choice of the individual in the case of the animal representative. A case for the fauna is by no means established, but, on the other hand, until either natural examples or experimental models prove conclusively that vegetation without meio- or macro-fauna can achieve this result, we must still reckon with the faunal element.

To advance towards the goal of a closer understanding, there is, in the writer's opinion, a need for greater cooperation with, and integration of, pedological and biological studies in all their aspects. Such a development should not mean a blind and indiscriminate resort to pedological methods, for example the correlation of fauna with such soil attributes as base status, water-stable aggregates, nutrients *etc.* This does not mean to say that these are not valuable measures, but rather that, owing to our scanty biological knowledge, it is similar to using an electron microscope when the conventional instrument would be very much better. In addition to chemical and physical we must consider *all* the biological aspects of this environment. Much has been gained from microbiological studies, but the time has come when we must expand and study in greater detail the other forms of life, the algae, actinomycetes, fungi, free-living nematodes, Arachnida and Insecta, amongst others. We must study the sum total of the living universe which inhabits the soil during the various stages of development. Let us remember that their influence is felt from the time when the first grains are formed on some weathered rock face, to the day many ages hence when a teeming mass of life, a vast complex both plant and animal, inhabit this milieu, and mould what is for mankind at one and the same time a production line and a storehouse for his sustenance and nourishment.

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DISCUSSION

MR. O. GILBERT (Nature Conservancy, Grange-over-Sands): Mr. F. Bocock and I are interested in the nutritional value of litter to litter-feeding animals, and at the moment we are giving our attention to the amino acids. Dr. W. R. Handley of Oxford has recently shown that the leaves of many trees, for example beech and oak, contain tanning compounds in their cell sap and that at leaf-fall the protein of the protoplast is tanned. On the other hand, the leaves of other trees, for example ash, contain little or no tannins. Tanning by vegetable agents is believed to affect the protein molecules largely through the basic amino acid residues, that is lysine, arginine and histidine, all three of which are indispensible for the development of animals. It is therefore possible that heavily tanned leaves do not constitute a 'square meal' for litter-feeding animals because they are deficient in these basic amino acids. Our preliminary analyses, which I must stress are very tentative, indicate that whereas newly fallen ash leaves contain histidine, this amino acid is virtually absent in hydrolysates of newly fallen oak and birch leaves.

PROFESSOR W. TISCHLER: One of the causes which lead to the 'mor' type of litter decomposition may be seen in the presence of certain antibiotics. As Winter has shown in a recent paper, antibiotic substances remain for a long time unchanged in ericaceous and coniferous plant residues and make bacterial life impossible. Thus an important basic group of the whole ecosystem is suppressed and the metabolic process is forced into another channel. In climatic areas with high rainfall the antibiotics of the needle litter are diluted, so that there, even under coniferous trees, 'mull' develops.

MR. J. HOBART (Department of Agricultural Zoology, University College, Bangor): I should like to refer to Bornebusch's figures for respiratory rate. Figures obtained in the laboratory are probably quite unreliable since the animals are removed from their normal environments. They probably, therefore, behave abnormally in response to stimuli. The difficulty of obtaining useful figures is very great.

DR. MURPHY: I am not in a position to comment on this adequately although I realize the drawbacks of figures obtained in the laboratory: I would refer you to Mr. Macfadyen. The Bornebusch figures quoted were used to demonstrate the general principles of the relationship between numbers, biomass and activity. Undoubtedly, in view of more recent developments, these data have many sources of error, but the relative differences do indicate the broad relationship of these characteristics in mull and mor.

MR. A. MACFADYEN: I have attempted to make a respirometer [see pages 442–443] in which animals may be subjected to diurnal rhythms of humidity and light. The whole problem requires a great deal of physiological analysis, but I agree with the general implication that, at the present time, respiratory activity cannot be used as a measure of ecological activity.